THE TAXONOMY OF POTAMOGETON SUBSECTION HYBRIDI IN NORTH AMERICA

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Potamogeton subsection *Hybridi* is a very distinctive group of small, linear-leaved Pondweeds. Especially characteristic of the group are stipules adnate to the leaf base with the free tip projecting as a ligule, the ability to fruit freely with or without floating leaves, and fruits with a conspicuous cochleate embryo. The unusual, flattened fruits distended by the easily visible spiral of the embryo are unique to this subsection.

The group is restricted to the Americas where it is widely distributed from Newfoundland south to Cuba and central Mexico and west to California and southern British Columbia. One representative is found in Brazil (Fernald, 1932, 1950; Hitchcock and Cronquist, 1973).

The general ecology of the North American species is similar in many respects. It is here briefly described as some ecological features are of importance taxonomically. The species usually occur in rather shallow water, growing near shores, in streams and in shallow ponds and bays. They are sometimes found in only a few inches of water. All will grow more or less exposed on mudflats and shores producing a terrestrial form with much shortened internodes and only dilated leaves. Observations in the field and examination of specimens indicate that all the species may be either annual or perennial in duration. They may perennate by persistent bases and rhizomes or by poorly differentiated winter buds.

From a taxonomic standpoint, the group has long been a source of considerable confusion. The number of species

recognized in North America in contemporary works varies from two, *Potamogeton spirillus* Tuckerman and *P. diversifolius* Rafinesque (Ascherson and Graebner, 1907; Taylor, 1909; Gleason, 1952), to four: *P. spirillus*, *P. diversifolius*, *P. capillaceus* Poiret and *P. bicupulatus* Fernald (Fernald, 1932, 1950). The difference in opinion as to the number of species is a result of the separation of *P. diversifolius* sensu lato into three species by Fernald (1932). Our investigation was prompted by the collection of a fine-leaved *Potamogeton* belonging to subsection *Hybridi* which was not previously known to occur in Canada. Initial attempts to name the specimens and related material proved unsatisfactory and further research was undertaken.

MATERIALS AND METHODS

This study is based on approximately 1850 specimens borrowed from the following herbaria: ACAD, CAN, DAO, ILL, GH, MIN, MO, NCU, TRT, NY, QK, TEX, UARK, US, USF, UWM, and the herbarium of the Algonquin Park Museum. In addition, populations of *Potamogeton spirillus* and *P. bicupulatus* were examined in the field in Canada.

THE SEPARATION OF POTAMOGETON SPIRILLUS

Potamogeton spirillus is regarded as distinct by all contemporary authors. Our observations have shown it to be easily distinguished from the other two taxa[1] of this group by a number of features. These features are summarized in Table 1. Figs. 1 and 2 illustrate the differences in the fruits and the degree of stipule fusion.

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[1]As will be shown subsequently, there are two other taxa in this subsection; a fine leaved northern plant called *Potamogeton bicupulatus* and a broader leaved, more southern species called *P. diversifolius*. They are referred to by these names in these and following figures.

Table 1: Distinction of *P. spirillus* *P. bicupulatus and* *P. diversifolius*

P. spirillus	*P. bicupulatus and* *P. diversifolius*
Fruits without lateral keels	Fruits usually with lateral keels
Fruits 1.3-2.4 mm in diameter	Fruits 0.9-2.0 mm in diameter
Peduncle of submersed spike up to 3 mm	Peduncle of submersed spikes 1-10 mm
Fused portion of stipules longer than free ligule	Fused portion of stipule shorter than free ligule
Phyllodal leaves 15-80 times longer than wide	Phyllodal leaves 20-500 times longer than wide
Phyllodal leaf tips usually rounded to subacute	Phyllodal leaf tips obtuse to setaceous

THE POTAMOGETON DIVERSIFOLIUS COMPLEX

Prior to Fernald's (1932) excellent work, two species were recognized in the subsection by monographers (Morong, 1893; Ascherson and Graebner, 1907; Taylor, 1909): (1) *Potamogeton spirillus*, incorrectly called by these authors *P. dimorphus*, and (2) *P. diversifolius*, incorrectly called *P. hybridus* by Ascherson and Graebner. The distinctions they used to separate the two were in the main those given here for separating *P. spirillus* from the other taxa.

Fernald (1932) greatly clarified the nomenclature and expanded the taxonomy of the subsection. He recognized three taxa other than *Potamogeton spirillus: P. diversifolius, P. capillaceus* and *P. bicupulatus*. These latter three species can be regarded as the *P. diversifolius* complex. *Potamogeton diversifolius* was treated as a wide ranging species with phyllodal leaves acute to obtuse and 0.5 to 2 mm wide, rounded dilated leaves and short peduncled submersed spikes. *Potamogeton bicupulatus* and *P. capillaceus* he recognized as similar to each other vegetatively,

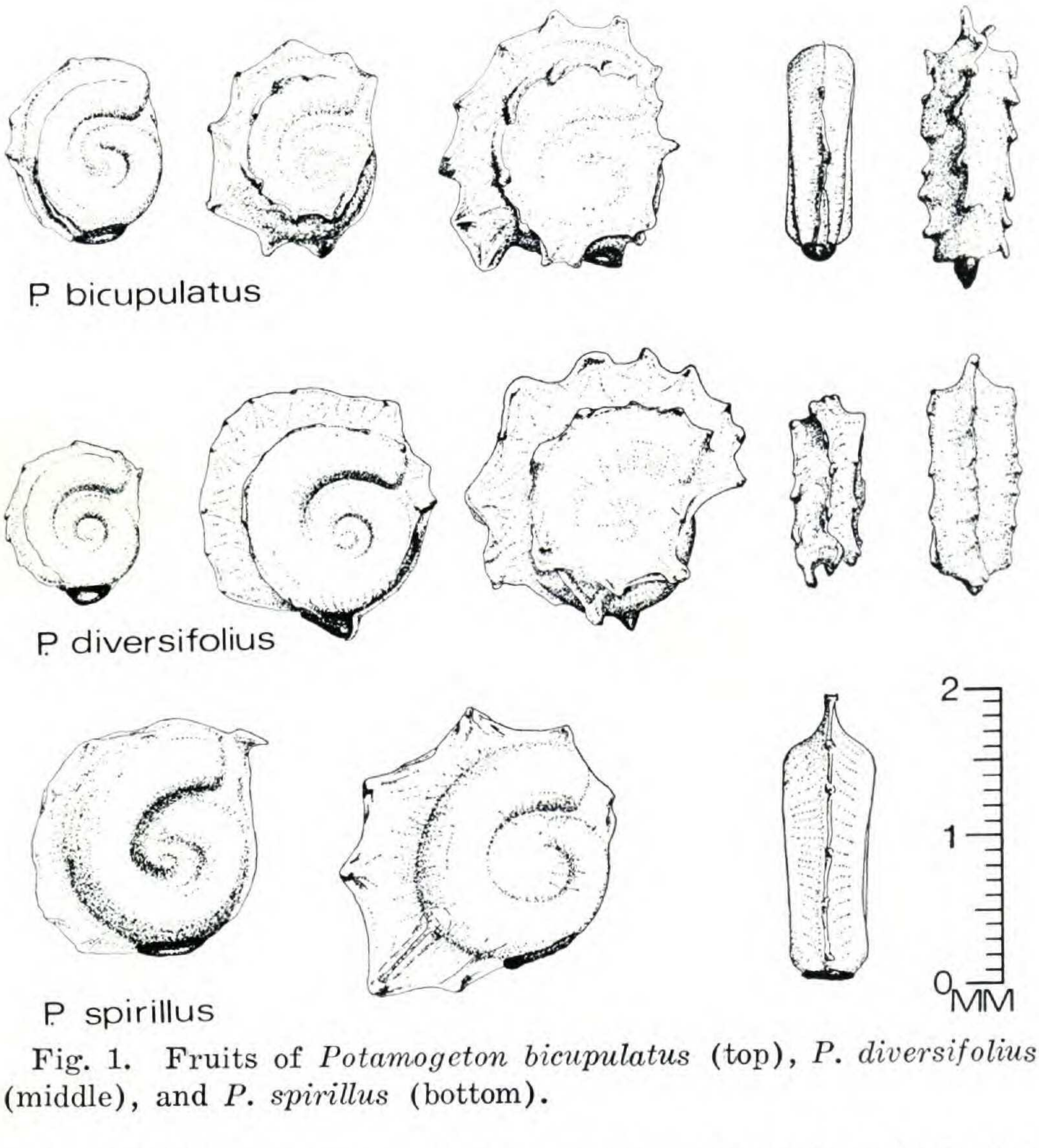

Fig. 1. Fruits of *Potamogeton bicupulatus* (top), *P. diversifolius* (middle), and *P. spirillus* (bottom).

and both differing from *P. diversifolius* in having phyllodal leaves setaceous, 0.1 to 0.6 mm wide, acute dilated leaves and longer peduncled submersed spikes. Fernald differentiated between the two on the basis of the fruits. *Potamogeton capillaceus* he considered a coastal species with flat sided olive fruits 1 to 1.5 mm wide and the former a rare plant of the Allegheny Mountains with 1.6 to 2.2 mm wide fruits that were stramineous with crateriform sides.

Klekowski and Beal (1965) investigated *Potamogeton capillaceus* and *P. diversifolius* in the Carolinas. They showed complete intergradation of the characters used to separate the two and presented strong evidence that it was

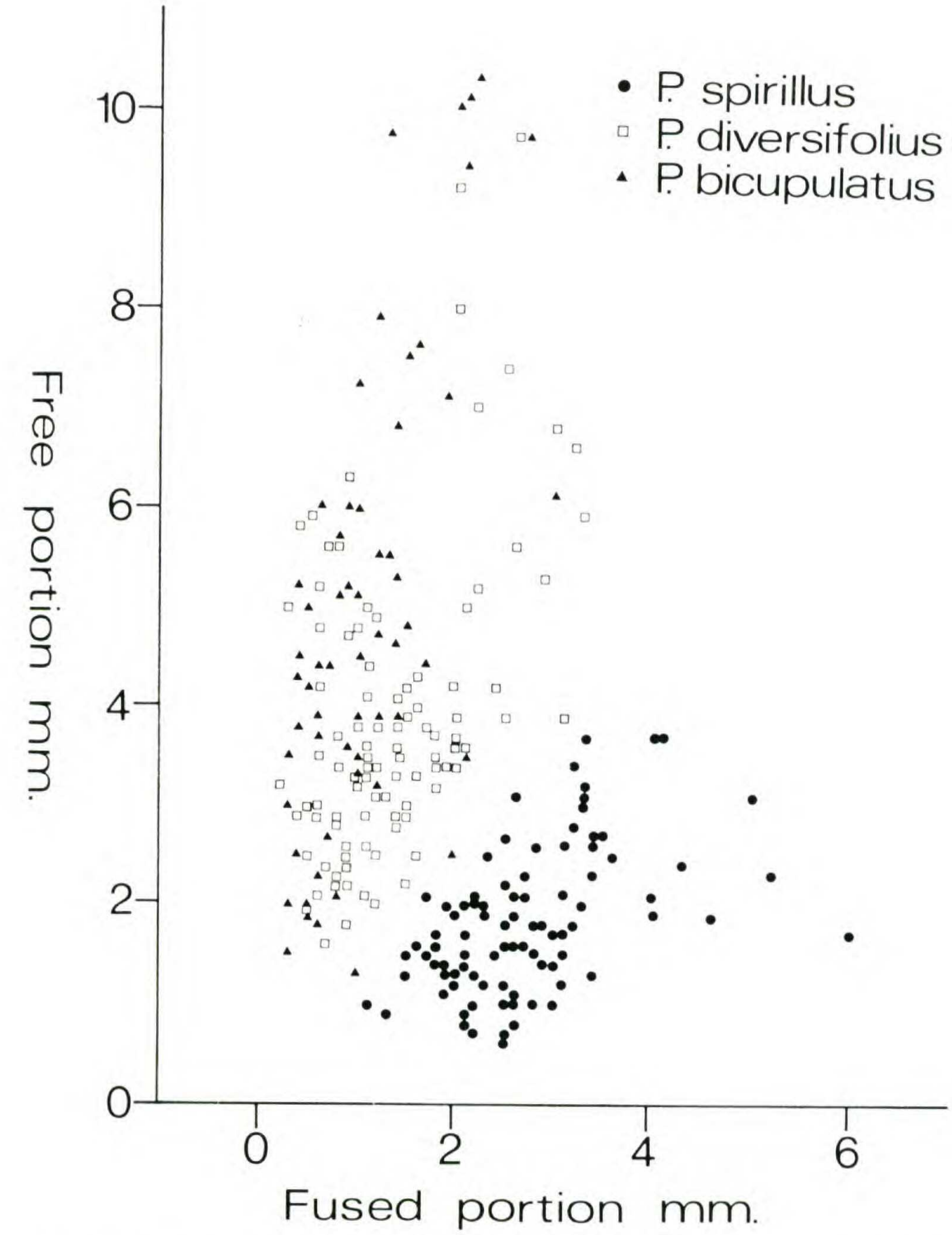

Fig. 2. Scatter diagram of length of free portion of stipule against length of portion fused with the leaf for *Potamogeton spirillus*, *P. diversifolius* and *P. bicupulatus*.

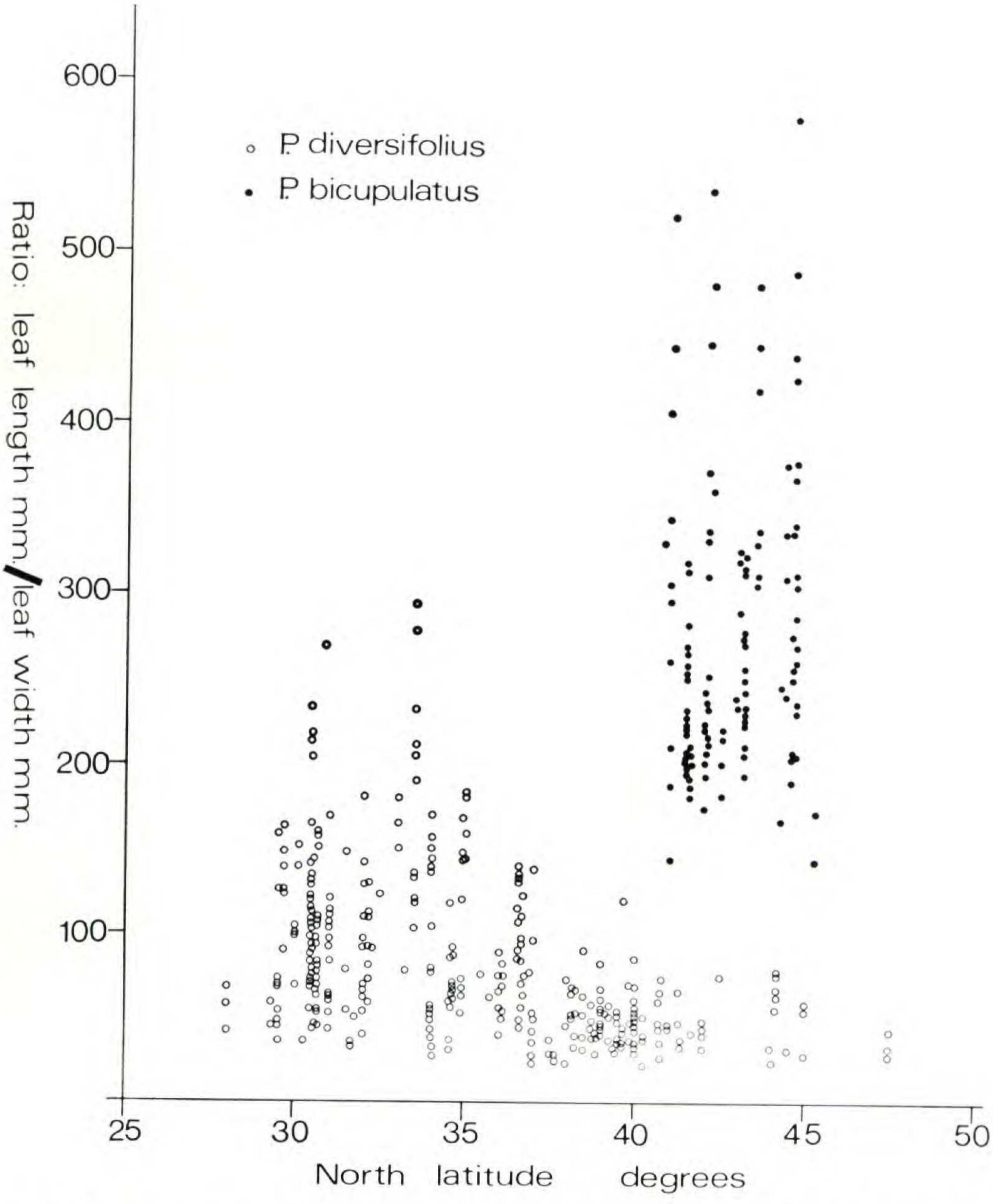

Fig. 3. Scatter diagram of phyllodal leaf length:width ratio against north latitude for *Potamogeton diversifolius* and *P. bicupulatus*.

not possible to recognize two taxa in the Carolinas. In spite of this evidence, Voss (1972b) felt that Michigan plants referable to *P. capillaceus* appeared distinct from *P. diversifolius*. These authors did not deal with *P. bicupulatus*.

When specimens of this complex were examined over their entire range, several most notable trends came to light. After a preliminary examination of many features, it was found that phyllodal leaf characters showed distinct discontinuities. These discontinuities were in leaf width, the leaf length-width ratio and the widest leaf present.

Figure 3 is a scatter diagram of leaf length:width ratios versus the latitude of the collection locality. Two clearly separate groups are illustrated. One is a very fine leaved northern taxon with leaf length:width ratios of about 200 to 600 that occurs from latitude 40 to 45 degrees north; the other a variable taxon that is wide ranging from latitude 25 to 48 (but generally more southern) and has a leaf length:width ratio of 30 to rarely more than 200. The two groups shown in Fig. 3 again separate clearly when the width of the widest phyllodal leaf is used in place of latitude (Fig. 4). Also, Fig. 5 shows a frequency diagram of leaf width. Again, two groups show as distinct entities. Other features such as dilated leaf length:width ratios and emersed spike length followed the same pattern but showed more overlap. We do not hesitate to recognize the two groups as different taxa at the specific level.

Fernald's annotations, and comparison of specimens with his descriptions, clearly indicate that the fine leaved northern plant was the major basis for his concept of *Potamogeton capillaceus*. The broader leaved southern plants are *P. diversifolius*.

Also clear from Fig. 3 is that wherever the two taxa occur at the same latitude, they do not approach each other in phyllodal leaf length:width ratio. Only where *Potamogeton diversifolius* occurs well south of the range of the northern fine leaved taxon do the values for this ratio approach each other. This is a very interesting displace-

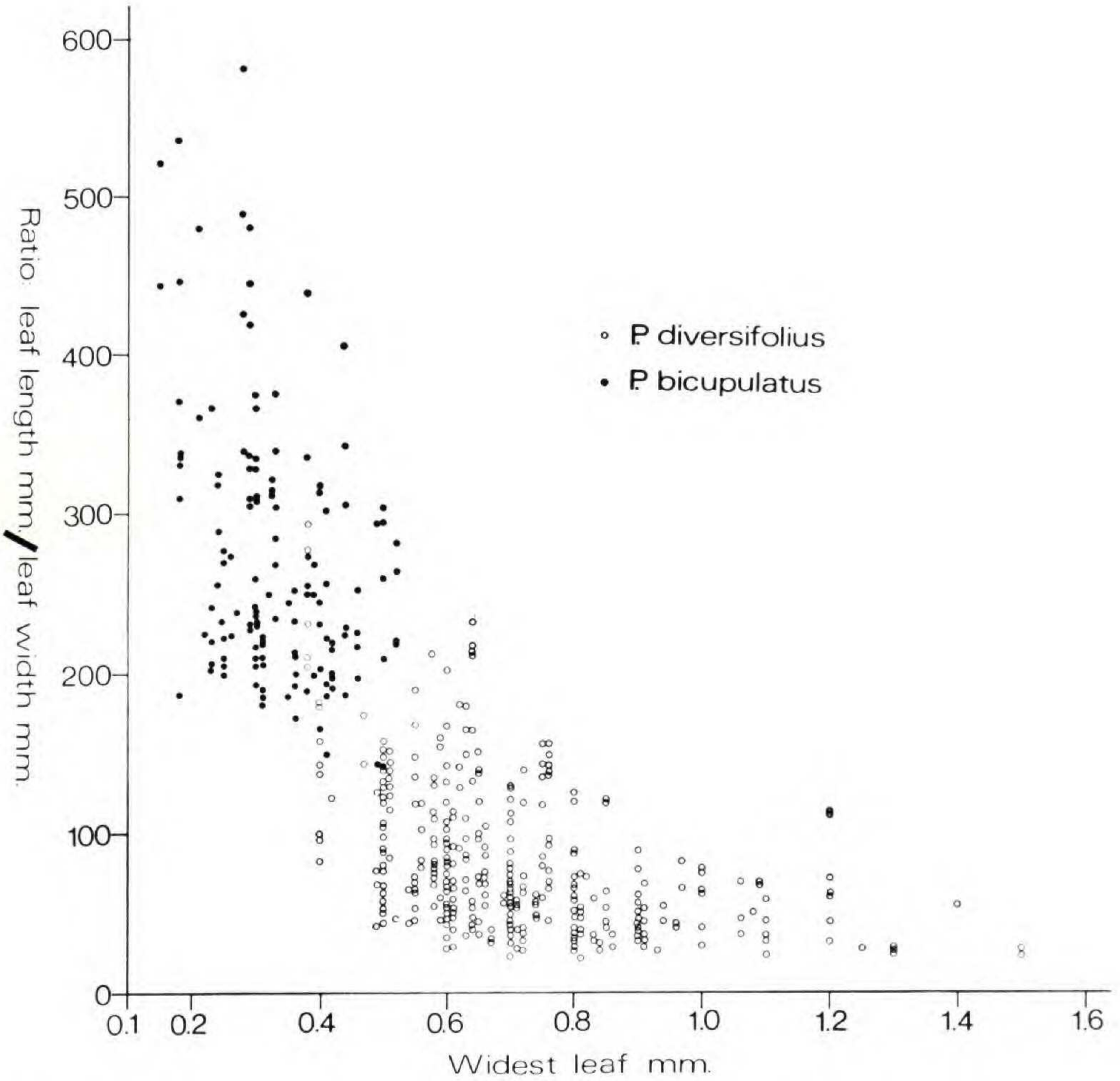

Fig. 4. Scatter diagram of phyllodal leaf length:width ratio against the widest phyllodal leaf for *Potamogeton diversifolius* and *P. bicupulatus*.

ment of characters. Fernald also considered *P. capillaceus* to include the finest leaved extreme of the southern plants. However, as Klekowski and Beal (1965) showed, they are indistinguishable from and merge completely with *P. diversifolius*. The only discontinuity shown in Fig. 3 occurs well north of the Carolinas.

That the southern plants are not merely more robust forms of the northern is clear. Figure 3 shows that there is a discontinuity of several degrees of latitude where there are no very fine plants. Secondly, there are rarely any actual overlaps in the measurements. Two specimens from

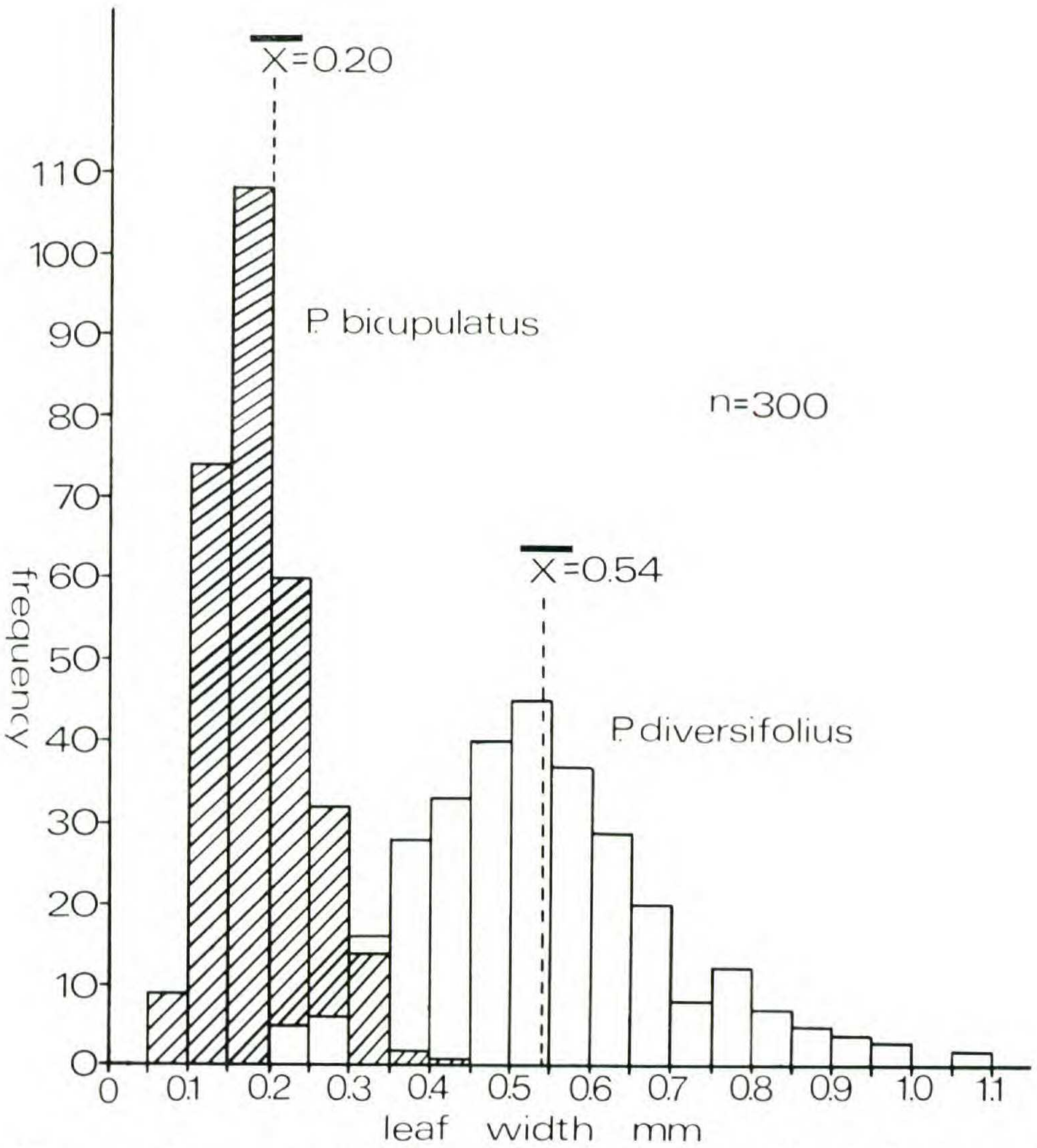

Fig. 5. Frequency histogram of phyllodal leaf width for 300 measurements each of *Potamogeton bicupulatus* and *P. diversifolius*.

the south were seen, both from lime sinks, that did overlap (*Radford* 7924, Florida, DAO; *Massey* et al. 2941, South Carolina, NCU). These two puzzling specimens are mostly responsible for what overlap there is in the graphs and are here considered rare extremes of *Potamogeton diversifolius*. Also, although there are considerable differences in the phyllodal leaves, the northern and southern taxa have fruits that are virtually identical in size. However, when finer leaved southern plants (widest leaf less than 0.6 mm) were measured, their fruits were distinctly smaller

(Table 2). This observation would not be expected if the southern fine leaved plants that Fernald (1932) considered *P. capillaceus* were more robust individuals of the northern fine leaved taxon. It indicates that the finer leaved southern plants are simply small extremes of *P. diversifolius*.

Table 2: Fruit diameters of *P. diversifolius* complex.

Species	Sample Size	Mean (mm)
P. bicupulatus	450	1.43
P. diversifolius		
Fine-leaved	128	1.36
Broad-leaved	322	1.42

THE IDENTITY OF POTAMOGETON BICUPULATUS FERNALD

Potamogeton bicupulatus was distinguished from *P. capillaceus* mainly by fruit size, color and sculpturing (Fernald, 1932). However, examination of specimens has not borne out the differences in color, and the sculpturing, based on the degree of development of the keels, was found to be extremely variable. No discontinuities were found in either feature. Figure 6 shows two frequency diagrams for fruit size for the northern fine leaved taxon and *P. diversifolius*. With a large sample it is easy to see that the fruits of the two species can range to extremes up to 2 mm. This is near the maximum size of 2.2 mm given for *P. bicupulatus* and well above the maximum of 1.5 mm stated by Fernald (1932) for *P. diversifolius* and *P. capillaceus*. Plants considered by Fernald as *P. bicupulatus* are extremes of fruit size and sculpturing.

The situation proved more complex when examined in detail. Fernald (1932) recorded three localities for his species: Vermont, Pennsylvania and Tennessee. The Vermont report was based on a single specimen (*Chapman*, s.n. Lake Dunsmore, Vt. (MO!). The specimen was doubted by Fernald and is clearly an error. The plant is *Potamogeton diversifolius* and unquestionably the locality is incor-

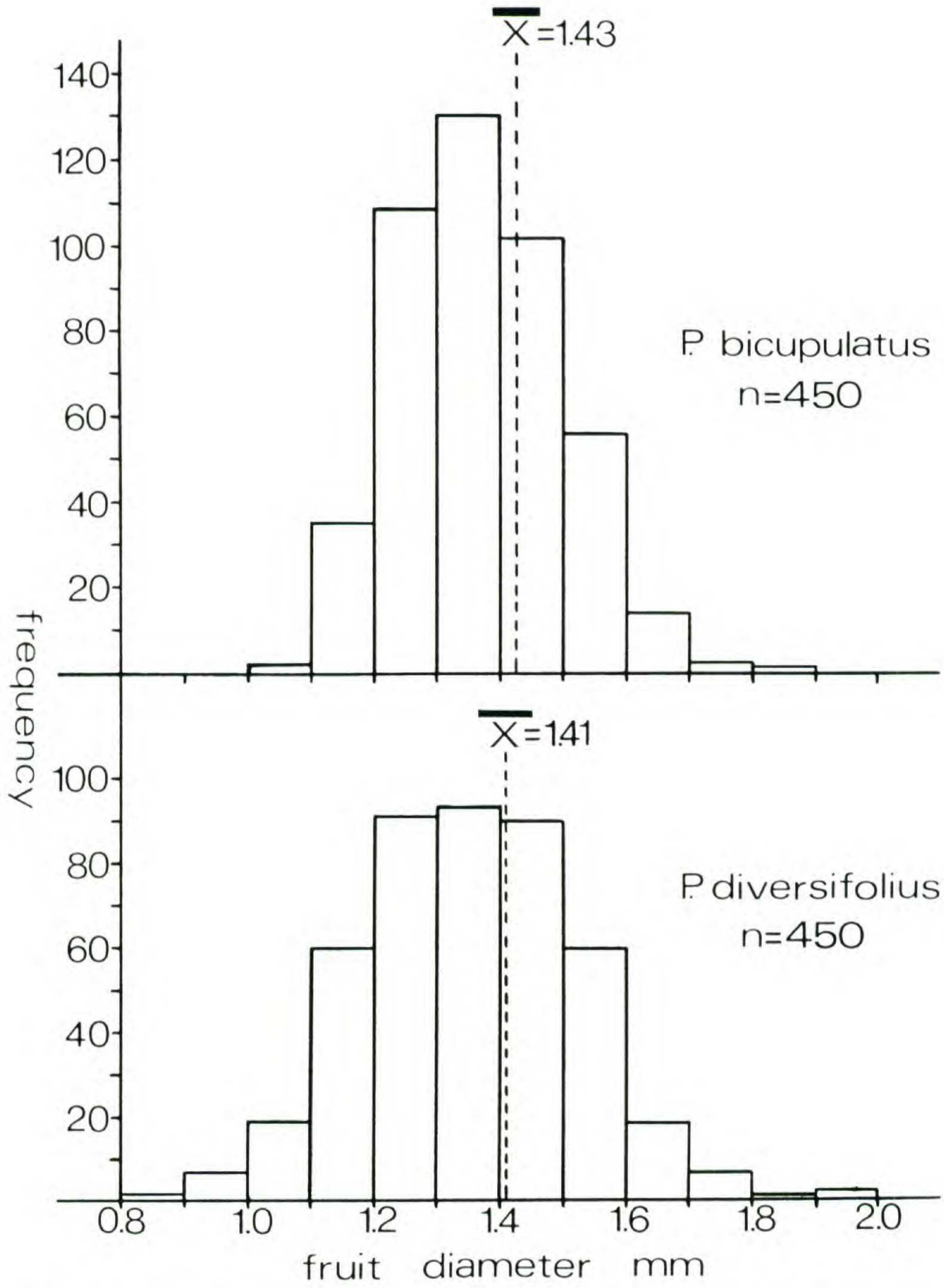

Fig. 6. Frequency histogram of fruit diameter for 450 measurements each of *Potamogeton bicupulatus* and *P. diversifolius*.

rect. When specimens from the other two areas were examined, it was found that the plants from Pennsylvania were exceedingly fine leaved with length:width ratios over 200 and the plants from Tennessee were wider leaved with length:width ratios well under 200. Figure 7 shows a frequency diagram of leaf width for plants from the two areas. When this is compared with Fig. 5 one can see that the Pennsylvania plants are clearly the northern fine leaved taxon and the Tennessee specimens are *P. diversifolius*. *Potamogeton bicupulatus*, as conceived by Fernald, consisted of localized populations of large fruited extremes of these two similar species. The name, however, applies to the northern fine leaved taxon as the type is from Pennsylvania.

NOMENCLATURE

Our investigations have confirmed Fernald's (1932) application of the names *Potamogeton spirillus* Tuckerman and *P. diversifolius* Rafinesque. The question of the correct name for the northern fine leaved taxon, however, must be settled. As discussed before, Fernald's concept of *P. capillaceus* was based mainly on this northern taxon. However, the type of *P. capillaceus* was stated to be from 'Caroline septentrionale' (Poiret, 1816). Voss (1972a) searched for this type and indicated that it might be in Herb. Desfontaines at Florence. Following his suggestion, this proved to be the case and when a photograph was obtained, the specimen was *P. diversifolius* with phyllodal leaves up to 0.8 mm wide. The name *P. capillaceus* must be relegated to synonymy under *P. diversifolius*.

A scrutiny of all available names revealed that the earliest name that applies to the northern fine leaved taxon is *Potamogeton diversifolius* var. *trichophyllus* Morong (type from New Jersey); however, the earliest name for the taxon applied at the specific level is *P. bicupulatus* Fernald (type from Pennsylvania). Fernald (1932) presented evidence that *P. dimorphus* Rafinesque (1817), based on *P.*

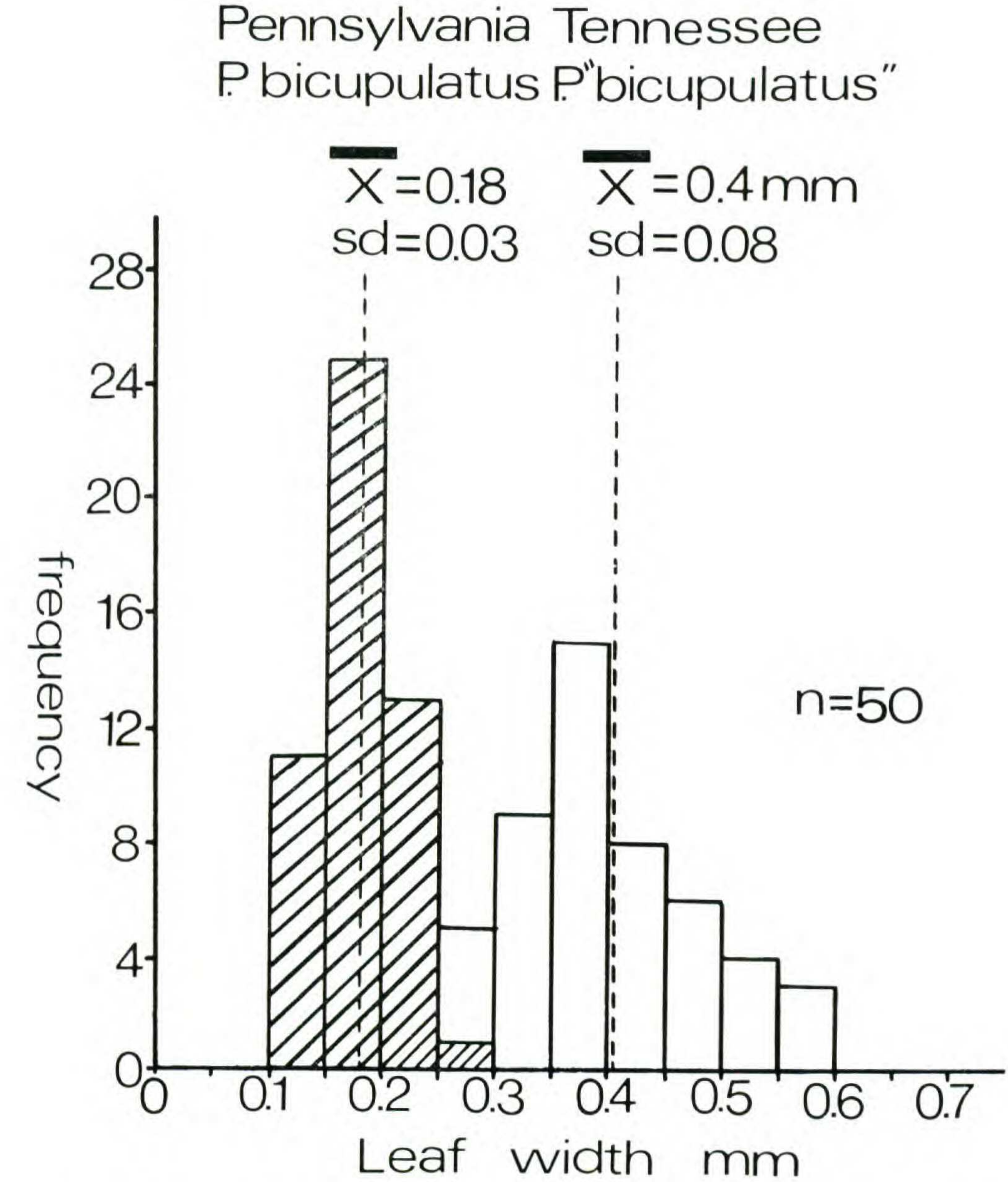

Fig. 7. Frequency histogram of phyllodal leaf width for 50 measurements each of Pennsylvania *Potamogeton bicupulatus* and Tennessee *P. "bicupulatus"*.

diversifolious W.P.C. Barton, also applies to the northern fine leaved taxon. However, he contrasts Barton's plant only with *P. spirillus* and does not mention the possibility of the plant being *P. diversifolius* Rafinesque nor for that matter his own *P. bicupulatus*. When the herbarium of W.P.C. Barton was consulted, there was no type. Pennell (1942) discusses the fact that the larger part of Barton's herbarium is lost. As all three species of this subsection occur in the Philadelphia region, there is no possibility of being completely certain of the application of the name with only the description given by Barton (1815). Without a type, the identity of *P. dimorphus* Rafinesque must be considered in doubt. We here use the oldest name at specific level whose application to the northern fine taxon is certain, *P. bicupulatus* Fernald. If the type of *P. dimorphus* Rafinesque should be found, that name may prove to apply here.

PRACTICAL TAXONOMIC DIFFICULTIES

Before the taxonomic treatment is introduced, it must be noted that some taxonomic difficulties encountered with these Potamogetons stem from problems in accurately observing the extremely fine parts of the plant. The widths of the phyllodal leaves ranged mostly from 0.1 to 1.0 mm and the lengths from 3 to 11 cm. On most collections, the very long, narrow leaves of the finest species were usually broken and almost invariably bent and folded. Accurate measurement of the dimensions required measuring to 0.01 mm for phyllodal leaf width and the use of extreme care to make sure that the full length of the leaf was intact. It was not possible to measure all specimens. Many poorer collections showed no complete leaves. The importance of good herbarium specimens in this group cannot be overemphasized.

Our experience indicates that the best technique for making specimens of these Potamogetons is to float the plants onto a more or less stiff sheet of well sized heavy

bond paper somewhat smaller than the herbarium sheet. After pressing and drying in the usual manner between newsprint, the sheet should be placed inside a large packet on the herbarium sheet. No glue need be applied to the plant.

When measuring specimens for identification, care must be taken to avoid leaves that are beginning to show a transition to dilated leaves. This transition is very gradual and easily overlooked. The first leaves of the year at the base of the plant, leaves that are from late fall shoots and proliferating shoots from the axils of floating leaves should also be avoided. The leaves to measure are mature leaves on the middle parts of main stems. Seedling plants of this group also may cause difficulties as they will be small in most measurements although they may bear fruit. Terrestrial forms and collections with only dilated leaves are often nearly impossible to determine. Flowing water forms also differ greatly in aspect but may usually be keyed out successfully. They do tend to have narrower leaves than usual.

KEY TO SPECIES[2]

1. Adnate portion of stipule mostly longer than free ligule, fruits with a dorsal keel and smoothly rounded sides. . . . . 1. *P. spirillus*

1. Adnate portion of stipule mostly shorter than free ligule, fruits usually with two lateral, entire to toothed ridges forming a 'shoulder' or row of teeth on either side of the dorsal keel.

    2. Middle stem leaves 190 to 500 times as long as wide, usually 0.1 to 0.35 mm wide, averaging 0.2 mm. . . . . 2. *P. bicupulatus*

    2. Middle stem leaves 20 to 180 times as long as wide, usually 0.3 to 1.5 mm wide, averaging 0.54 mm. . . . . 3. *P. diversifolius*

[2]The term leaf as used in the key refers to the phyllodal leaves.

TAXONOMIC TREATMENT[3]

1. *Potamogeton spirillus* Tuckerman, Amer. Jour. Sci. and Arts, Ser. 2, 6:228, 1848. Type locality: Charles and Mystic Rivers, Massachusetts. Type not traced.

Plant up to 10 dm, bushy at base, mostly with a few elongate stems, these sparsely branched; with or without dilated leaves. Dilated leaves 7-35 mm long, 2-13 mm wide, lanceolate-elliptic to elliptic-ovate, obtuse, tapering to rounded at base with 5-13 veins strongly impressed beneath; petiole 5-25 mm. Stipules of dilated leaves 3-15 mm, membranaceous to ± fibrous, free from leaf base. Phyllodal leaves 8-80 mm long, 0.5-2 mm wide, linear, flat, 15-80 times as long as wide, rounded to acute, 1-3 veined, usually with a lacunar band bordering midvein. Stipules 2-12 mm, membranaceous, fused with the leaf for 1.5-6 mm, fused for half or more of the total length. Fruiting spikes dimorphic, spikes in the axils of phyllodal leaves 2-5 mm in diameter, 1-8 fruited, globular; peduncle up to 3 mm, recurved. Transitional to spikes in the axils of dilated leaves; these 4-13 mm long, 4-5 mm wide, 4-35 fruited, ellipsoid to cylindric; peduncles 4-27 mm, slightly clavate. Fruits 1.3-2.4 mm in diameter, ± orbicular, olive-green to stramineous, flattened, keeled. Dorsal keel entire to sinuate, lateral keels absent. Beak minute. Fruit concave sided, distended by the cochleate embryo.

The distribution of this common northern species is mapped in Fig. 8. Tuckerman's excellent description of the plant is very clear and he carefully contrasted his plant with *Potamogeton bicupulatus* (sub *P. hybridus* Michaux), the only other related species occurring in Massachusetts. There is no doubt that his name applies to this distinctive little pondweed.

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[3]Synonymy is cited only where it differs from that given in Fernald (1932).

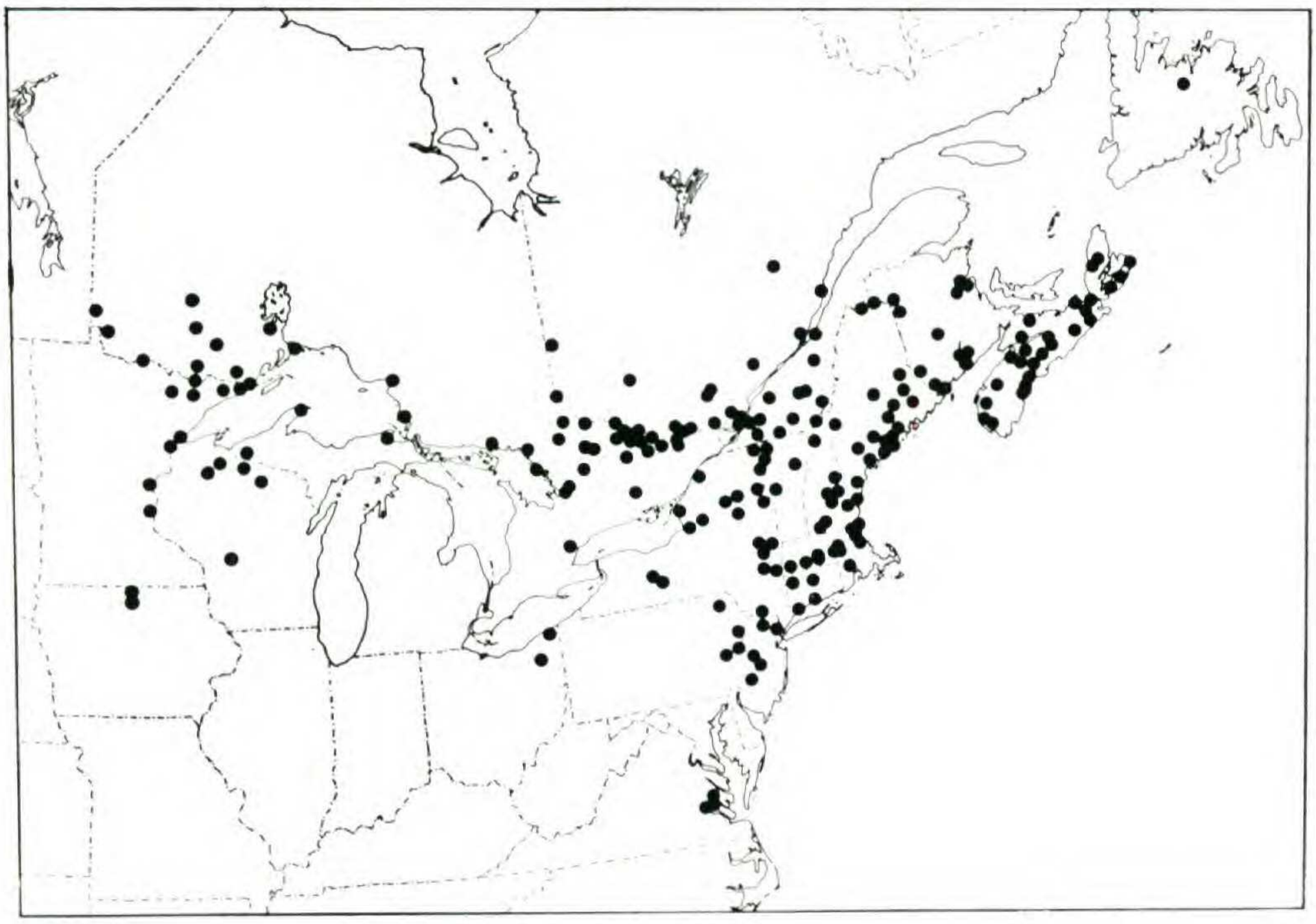

Fig. 8. Distribution of *Potamogeton spirillus*.

2. *Potamogeton bicupulatus* Fernald, Mem. Am. Acad. **17**: 112, 1932. Holotype: Lehigh Co., Pennsylvania, *A. P. Garber* 1866 PH, photo TRTE(!). Probable isotypes: GH(!), QK(!). (These specimens bear the additional data: Lehigh water gap, Blue Mts.)

P. diversifolius Raf. var. *trichophyllus* Morong, Mem. Torr. Bot. Club. **3**: 49, 1893. Holotype: Lake Marcia, Sussex Co., New Jersey, *N.L. Britton*, Aug 31, 1883. NY(!).

Plant up to 11 dm, bushy at base, mostly with a few elongate stems, these sparsely branched; with or without dilated leaves. Dilated leaves 6-23 (28) mm long, 2-11 mm wide, lanceolate-elliptic to broadly elliptic, acute, tapering to rounded at base with 3-7 veins strongly impressed beneath; petiole 5-35 mm. Stipules of dilated leaves 3-11 mm, membranaceous, free from leaf base. Phyllodal leaves 30-110 mm long, 0.08-0.4 (0.5) mm wide, setaceous, 190-500

(600) times as long as wide, long acuminate to setaceous, 1 veined. First leaves of the season, leaves transitional to dilated leaves and leaves of shoots produced late in the fall may be shorter and wider, sometimes as little as 140 times as long as wide. Stipules 2-12 mm, membranaceous fused with the leaf for 0.3-3.5 mm, fused for less than half of the total length. Fruiting spikes dimorphic, spikes in the axils of phyllodal leaves 1.5-7 mm long, 1.5-5 mm wide, 1-15 fruited, globular to ellipsoid, peduncle 1-10 mm, ± recurved, clavate. Transitional to spikes in the axils of dilated leaves; these 3-14 mm long, 2.5-4.5 mm wide, 5-40 fruited, ellipsoid to cylindric; peduncle 3.5-22 mm, slightly clavate. Fruits 1.1-2.0 mm in diameter, ± orbicular, olive-green to stramineous, flattened, keeled, dorsal keel entire to dentate, two lateral keels usually present, often consisting of isolated teeth, sometimes entire. Beak minute. Fruit concave sided, usually distended by the cochleate embryo.

This very delicate pondweed is illustrated in Fig. 9a and its distribution mapped in Fig. 10. Although mainly eastern, it has outlying stations near Georgian Bay, Ontario, at the head of Lake Michigan in Michigan and Indiana and in central Wisconsin and Minnesota. This is a distribution pattern shown by many more coastal species (Peattie, 1922; McLaughlin, 1932). In Ontario, *Potamogeton bicupulatus* occurs in the shallow soft water of Canadian Shield Lakes with peaty or sandy bottoms. These lakes are notable for the large number of rare and unusual aquatic plants that they possess. As well as *P. bicupulatus*, included are: *Isoetes macrospora, Potamogeton oaksianus, Eleocharis robbinsii, Juncus militaris, J. pelocarpus, Eriocaulon septangulare, Elatine minima, Myriophyllum tenellum, M. farwellii, Nymphoides cordata, Gratiola aurea, Utricularia resupinata, U. purpurea* and *Littorella americana.*

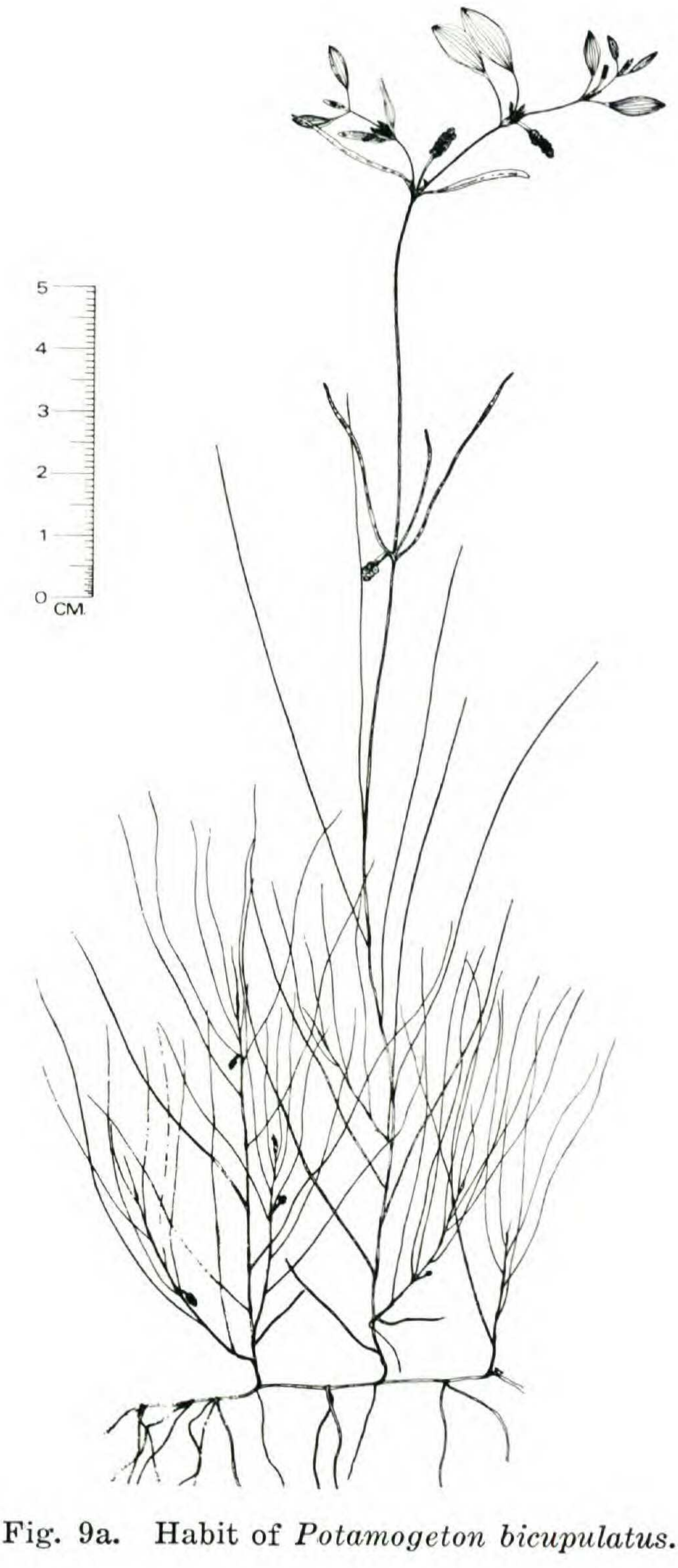

Fig. 9a. Habit of *Potamogeton bicupulatus*.

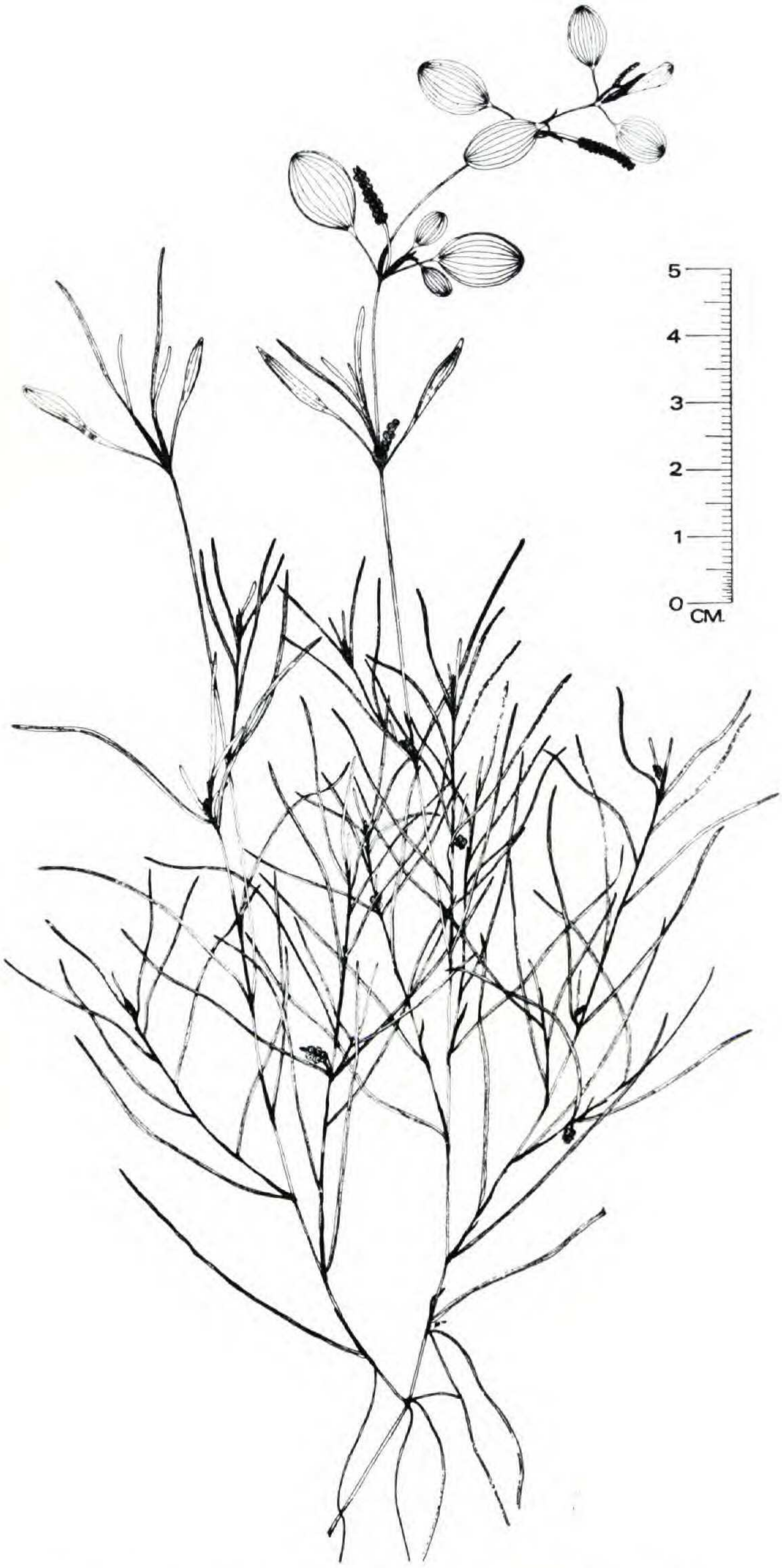

Fig. 9b. Habit of *Potamogeton diversifolius*.

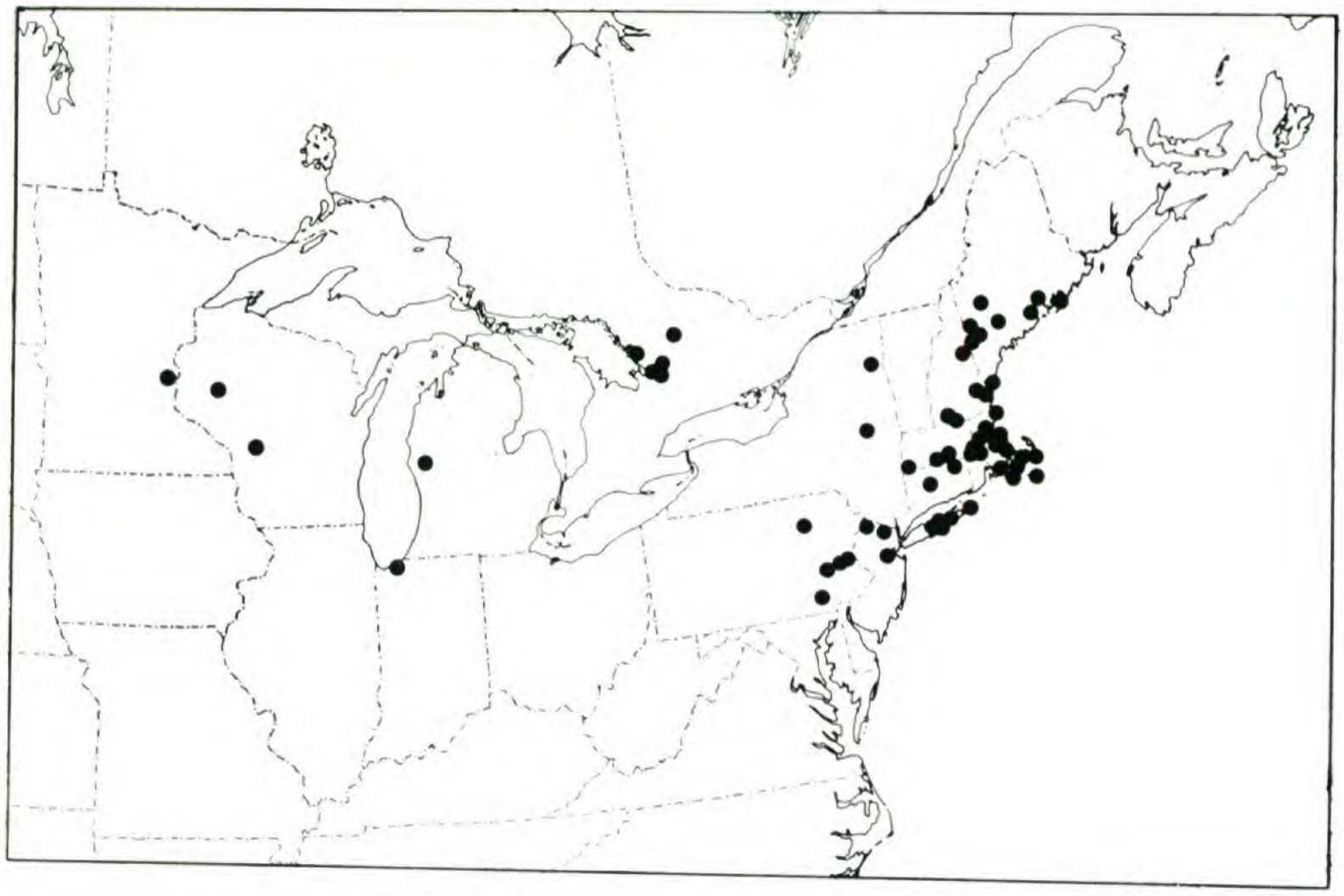

Fig. 10. Distribution of *Potamogeton bicupulatus*.

3. *Potamogeton diversifolius* Rafinesque, Med. Repos. 2. **5:** 354, 1808. Based on *P. hybridus:* var. β Michaux, Fl. Bor. Am. **1:** 101, 1803. Holotype in Herb. Michaux: In stagnis Carolina, *Michaux*. P n.v.

P. capillaceus Poiret, Encyc. Meth. Bot. Suppl. **4:** 535, 1816. Holotype in Herb. Desfontaines: Caroline septentrionale, *M. Delisle*. FI, photo TRTE (!). (Original label missing from specimen.)

P. diversifolius var. *multidenticulatus* Morong, Mem. Torr. Bot. Club **3:** 48, 1893. Holotype: Rehoboth City, Delaware, *G. F. Parker*, Aug. 17, 1878. NY (!).

P. capillaceus var. *atripes* Fernald, Rhodora **39:** 380, 1937. Holotype: Jones Hole Swamp, Coddyshore, Sussex Co., Virginia, *Fernald & Long* 5976, July 20, 1936. GH (!). Isotypes: NY (!), US (!), MO (!).

Plant up to 15 dm, ± bushy at base, mostly with elongate, ± branched stems; with or without dilated leaves. Dilated leaves 5-40 mm long, 2-20 mm wide, lanceolate-elliptic to ovate or obovate to suborbicular, acute to rounded, tapering to rounded at base with 3-17 veins

strongly impressed beneath; petiole 2-40 mm. Stipules of dilated leaves 2-25 mm, membranaceous to ± fibrous, free from leaf base. Phyllodal leaves, 10-80 (110) mm long, (0.25) 0.35-1.5 mm wide, linear, flat, 20-150 (280) times as long as wide, obtuse to long acuminate, 1 (3) veined, larger leaves with a lacunar band. Stipules 2-18 mm, membranaceous, fused with the leaf for 0.3-4.0 mm, fused for less than half of the total length. Fruiting spikes dimorphic, spikes in the axils of phyllodal leaves 1.5-6 mm long, 1.5-5 mm wide, 1-15 fruited, globular to ellipsoid; peduncle 1-8 mm, ± recurved, slightly clavate. Transitional to spikes in the axils of dilated leaves; these 3-28 mm long, 2.5-5 mm wide, 5-120 fruited, ellipsoid to cylindric; peduncle 3-32 mm, slightly clavate. Fruits 0.9-2.0 (2.2) mm in diameter, ± orbicular, olive-green to stramineous, flattened, keeled, dorsal keel entire to dentate, two lateral keels usually present, entire to dentate. Beak minute. Fruit flat sided to concave, often distended by the cochleate embryo.

This wide ranging *Potamogeton* is illustrated in Fig. 9b and its distribution mapped in Fig. 11. Fernald's (1937) *P. capillaceus* var. *atripes* is here not considered worthy of separation, the black, rigid rhizomes being certainly a result of the plants' anomalous habitat.

We have also found, as did Klekowski and Beal (1965), that the narrowest leaved plants of *Potamogeton diversifolius* tend to occur on the coastal plain. This trend is especially evident, judging from herbarium records, on the gulf coastal plain. However, as Klekowski and Beal (1965) showed, they merge completely with broader leaved *P. diversifolius* and are here not viewed as a separate taxon.

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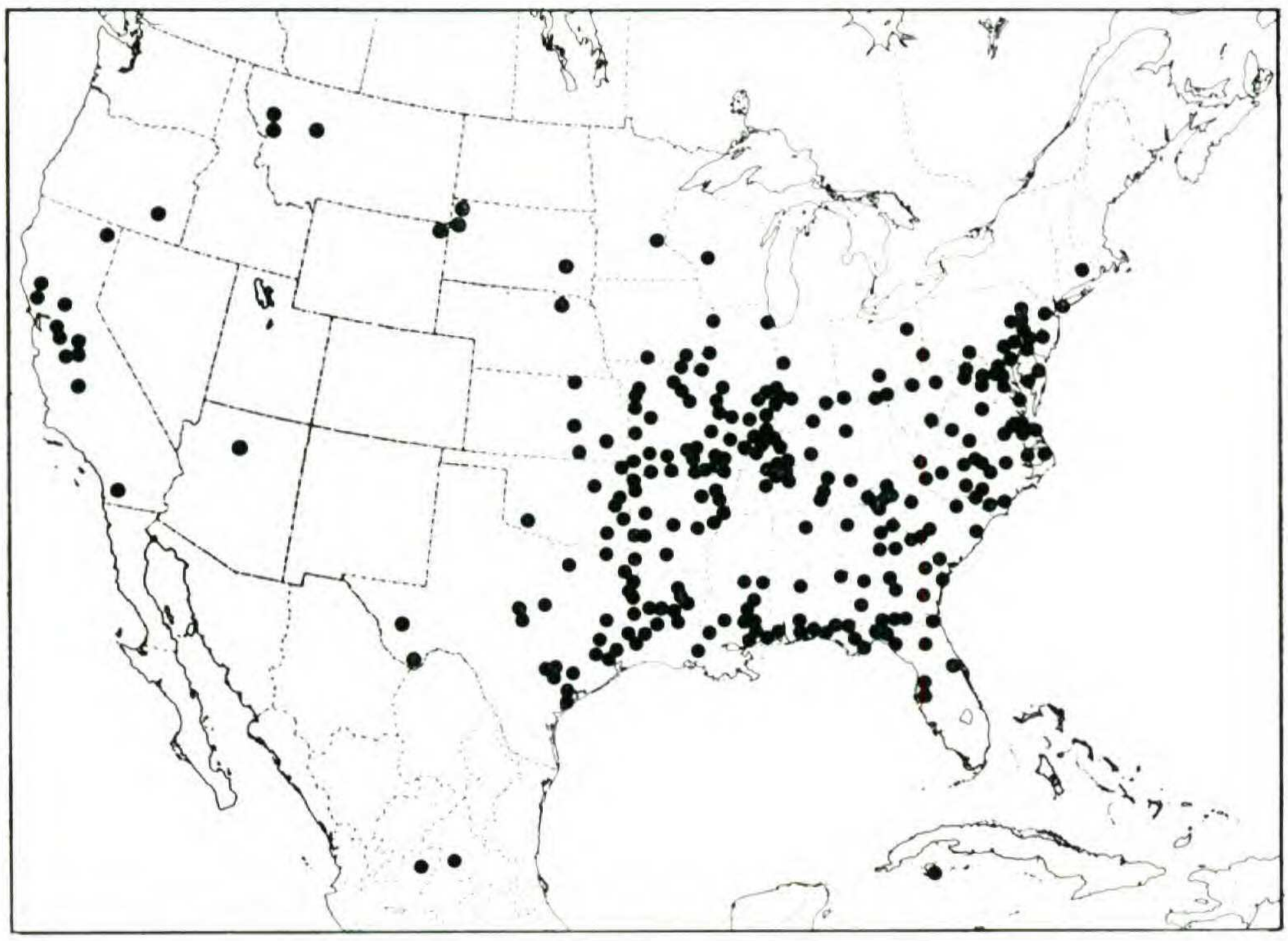

Fig. 11. Distribution of *Potamogeton diversifolius*.

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